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On the aggregational habits of surface dwelling Collembola

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With 3 figures

1. Introduction

Numerous investigations performed on the distribution patterns of Collembola pointed out that Collembola, like most populations of soil animals have an aggregated distribution. These conclusions are mostly based on statistical descriptions of the distribution pattern (Kaczmarek 1960; Poole 1961, 1962, 1964; Hale 1966; Usher 1969 and Joosse 1970). A correlation with some environmental factors reveals that the springtails are concentrated in humid places within their habitat (Poole 1962, 1964; Joosse 1970). It is generally thought that these aggregational habits are important for the survival of these less drought-resistant species and this is sustained by the fact that surface dwelling species with a low resistance to drought have a highly aggregated distribution pattern (Joosse 1970).

It has been known for a long time that insects are very sensitive to dry conditions during moult (Wigglesworth 1948). Collembola moult frequently, throughout their life, so they face the problem of water loss very often. One can imagine that the survival value of aggregations must be particularly high during these sensitive stages in the development of the animals.

In the experiments described here we have tried to demonstrate the biological significance of the statistically described aggregations of Collembola.

2. Materials and methods

The experiments were carried out in the laboratory with two litter-dwelling species: *Orchesella cincta* (Linné) and *Tomocerus minor* (Lubbock). The species were collected in a pine plantation, where they live together.

The distribution pattern of the animals was described in an artificial semi-natural habitat, consisting of a wooden tray of 40 cm square, provided with a bottom of plaster of Paris, on which a piece of woodland was built up. The material was taken from the habitat where the species originally occurred. The animals were released in the centre of the habitat.

Aggregations were statistically defined according to the method of Usher (1969). This method relies on the use of two basic statistics, the mean (m) and the variance (s^2). It is a property of a random (Poisson) distribution that the variance and the mean are equal, or in practice, not significantly different. A large ratio s^2/m indicates aggregation and the significance of departure from unity (random) can be tested by $\chi^2 = s^2/m\,(n - 1)$, with $n - 1$ degrees of freedom. The X^2-criterion was calculated to determine the randomness of the distribution in the semi-natural habitat. Therefore this habitat was sampled in 16 equal units of 10 cm square, by a rapid introduction of small metal strips. The analysis then proceeds by locating aggregations, eliminating these from the data and testing the residual-distribution again, until it is not significantly different from a random distribution.

As aggregated distributions have a variance greater than the mean, the coefficient of dispersion s^2/m increases with increasing m. For this reason the quotient $\log s^2/\log m$ was used when a comparison of distribution patterns based on different densities was necessary (Taylor 1961).

The stages in the moulting and reproduction cycles of the animals used in the experiments were observed in glass boxes. The animals were fed with *Pleurococcus* sp. (green algae), taken from the bark of trees. The algae were mixed in water. A suspension of this mixture was presented in drops on small strips of filter paper. The temperature was 15 °C.

3. Results

3.1. Laboratory experiments on the nature of aggregations

A first experiment was designed to determine whether these collembolan species show an aggregated distribution in the semi-natural habitat and to relate this pattern to moulting and reproduction phenomena. In a second experiment the changing distribution in time of a group of specimens that were synchronized in their moulting rhythm was studied. Synchronization can be performed easily by introducing a starvation period. After subsequent food supply the animals moult **simultaneously** after 6 days (Joosse and Veltkamp 1970).

In the first experiment 109 specimens of *Orchesella cincta* and 80 of *Tomocerus minor* were released in the centre of the habitat. After 7 days it was determined whether the animals were aggregated and the number of aggregates was established according to the method of Usher (1969). The recapture amounted to 75% for *O. cincta* and 93% for *T. minor*. The distribution appeared to be aggregated and in both species two aggregations could be dinstinguished, situated in adjacent units. So in fact perhaps only one clump was formed. The number of aggregated and non-aggregated individuals is given in table 1.

The aggregated and non-aggregated animals were next put separately in glass jars. After 3 days the percentage of moulted specimens and the number of eggs produced was established. As *T. minor* eats its exuviae, moulting data are only present for *O. cincta*. The Results are presented in table 1.

Table 1 The nature of aggregated and non-aggregated individuals of *O. cincta* and *T. minor*

	Orchesella cincta		*Tomocerus minor*	
	aggregated ind.	non-aggregated ind.	aggregated ind.	non-aggregated ind.
number	25	57	20	54
nr. of eggs	20	0	101	0
% moulted	76	0	?	?

From this experiment there seems to be evidence that animals in aggregations are to a large extent in a similar stage with respect to their moulting and reproduction cycle.

For the second experiment a large number of synchronized specimens of *O. cincta* were divided in 5 groups. One group of 100 individuals was put in jars to determine the moulting data and the locomotory activity. This was done by a frequent observation of the number of animals showing locomotory activity (Joosse and Groen 1970). Four other samples were put into 4 artificial habitats as described before. In these habitats the degree of aggregation was determined from the 5th to the 21st day. Moreover two descriptions of the aggregation pattern of unsynchronized animals were available. The experimental scheme is presented in fig. 1, the results in fig. 2.

It can be seen that during the first moult on the 6th day after starvation a high aggregation occurs and that this coincides with a low locomotory activity. The activity increases gradually until about the 9th day, when no aggregation occurs. Before the second moult a decreasing activity can be noticed and an increasing aggregation. But as a result of a rather high variation in the duration of the moulting instars, which is different for males and females, for reproductive and non-reproductive instars and for different ages (Joosse et al. 1973), the synchronization effect is already less apparent at the second moult. As a result the

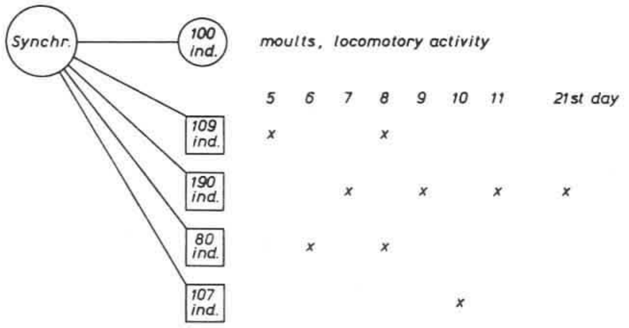

Fig. 1. Experimental scheme for the description of aggregations in relation to moulting in *Orchesella cincta*.

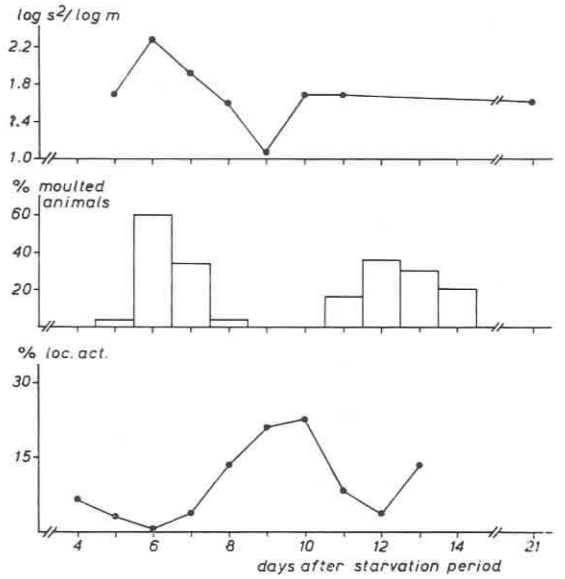

Fig. 2. Relation between distribution, moulting and locomotory activity in *Orchesella cincta*.

aggregation coefficient reaches an average, constant value, which is similar to the value obtained at the 21st day and that obtained with unsynchronized individuals (1.6).

This changing distribution pattern, which coincides with a changing moulting stage contributes again to the idea that a statistically described aggregation consists of biologically equivalent animals, being in the same stage of their moulting cycle.

3.2. The formation of aggregations

Collembola are in general very sensitive to dry conditions. It has been demonstrated that this sensitivity is species specific and that dry conditions stimulate the animals to locomotion: when the conditions are dryer, they move more rapidly (Joosse and Groen 1970). So in general Collembola react to conditions of drought by intensifying their mobility, by which they automatically reach damp places, where they slow down and become motionless.

In fig. 2 it was shown that locomotion of collembolan species also varies within one moulting instar. Thus one can come to the conclusion that this fluctuating activity is induced by a fluctuating sensitivity to drought during the moulting instar. Verhoef and Joosse (in

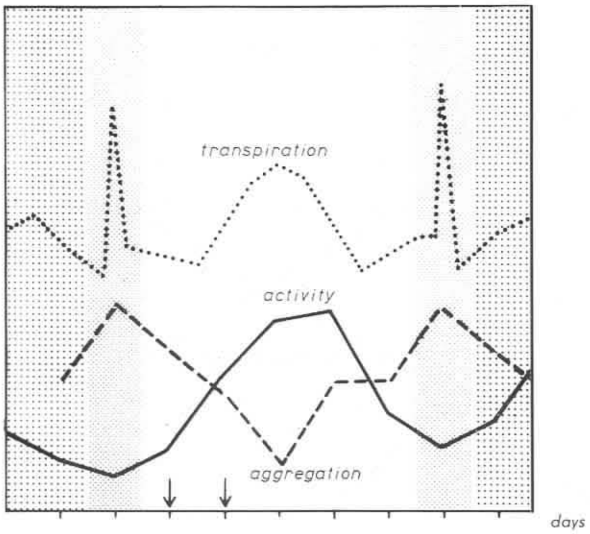

Fig. 3. Variation of aggregation, locomotory activity and basic transpiration pattern in *Orchesella cincta* during one moulting instar.

▨ = moult

░ = feeding

↓ ↓ = egg production

preparation) demonstrated that indeed the loss of water per unit of time varies during the moulting instar. In fig. 3 these data are used to build up a concept of the formation of moulting aggregations. During the moult the animals are aggregated, their locomotory activity is low, their basic transpiration pattern very high. That means that they lose relatively much water during that time. The transpiration was established in resting animals, so the increasing transpiration during the intermoult is not caused by the increasing activity. The interpretation then may be that an increasing water loss per unit of time in an individual results in an increasing sensitivity to drying conditions, which stimulates the locomotory activity. As a result of this phenomenon they automatically move to places with higher humidities, where they come to rest before the next moult. As each individual reacts in the same way, some damp places in the environment are occupied for a great part by these most sensitive stages. This is in agreement with the results of the experiments (3.1.). Although after some severe environmental conditions a synchronization could be established in field conditions (Joosse 1974, in press), field populations are in general not synchronized with respect to their moulting cycle. This means that aggregations which are continuously present in field conditions, contain always different individuals of a definite stage in their development.

4. Summary

Most Collembolan populations are non-randomly distributed in their habitats. The causes of these distributions are found in a high sensitivity to drought, which leads to a preference for humid places. The individuals of the population are present in clusters especially during their moulting- and reproduction stages. This is realized by a fluctuating sensitivity to drought during their life. It is concluded that an aggregated distribution has an important survival value especially for these delicate stages in the development.

5. References

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